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Secondary Production and Dietary Preference in Orconectes Propinquus (Girard)

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SECONDARY PRODUCTION AND DIETARY PREFERENCE IN ORCONECTES PROPINQUUS (GIRARD)

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TABLE OF CONTENTS

LIST OF ILLUSTRATIONS

LIST OF TABLES

ABSTRACT

A laboratory study was conducted to assess how three dietary components available to crayfish in a Southwestern Lake Michigan rock site affect secondary crayfish production. Three size classes of O. propinquus were fed ad libitum from 1 of 4 food treatments: algae, macroinvertebrates, detritus, or a combination of the three, for 61 days. Changes in wet weight and cephalothorax length were monitored every five days. Individuals of size class I grew more rapidly when fed combination and macroinvertebrate food treatments, than when fed detritus or algae. Size classes II and III maintained weight with no significant effect of food treatment on growth. In dietary preference studies, O. propinquus were offered equal volumes of algae, macroinvertebrates, and detritus simultaneously. While O. propinquus showed a strong preference for a macroinvertebrate diet, crayfish collected from the rock site fed extensively on algae, indicating that secondary production may be limited by food availability at the rock site.

CHAPTER I

INTRODUCTION

The nearshore waters of southwestern Lake Michigan are littered with rocky areas that extend from approximately 6 m to 20 m depth (Janssen and Quinn 1985). Two species of crayfish, *Orconectes propinquus* Girard and *Orconectes virilis* Hagen, are the dominant benthic macroinvertebrates in the rocky areas of southwestern Lake Michigan's littoral zone (Janssen and Quinn 1985). What sustains these crayfish is in question since the four major dietary components of crayfish documented in other systems, macroinvertebrates (Mason 1974), macrophytes (Lodge and Lorman 1987), macroalgae (Mozley and Howmiller 1977) and detritus (Prins 1968) are scarce or nonexistent in this habitat. Although light and nutrients are high enough to support low-density epilithic periphyton communities, macrophytes are absent. Further, the abundance of non-crayfish macroinvertebrates (insect larvae, isopods, amphipods, and gastropods) is seemingly insufficient to support the crayfish populations. Despite these apparent resource limitations, crayfish densities in the rocky areas are remarkably high. Momot *et al.* (1978) also reported crayfish as dominant invertebrates in ecosystems in which availability of benthic food sources were low, and suggested they survived on microbially conditioned dead wood.

Preliminary studies of the gut contents of crayfish from the rocky areas of the southwestern Lake Michigan littoral zone showed benthic algae to be a major component of the crayfish diet (58% of gut content biovolume) (Table 1). It was, therefore, hypothesized that in Lake Michigan, the crayfish were exploiting all sources of benthic food, but algae with high turnover rates largely supported the high crayfish population densities. This study examined crayfish growth on the dietary components available to them in the rocky areas of the southwestern Lake Michigan littoral zone. The objectives of this study were:

(1) to determine how growth rates of *O. propinquus* varied when crayfish were reared on diets of exclusively algae, macroinvertebrates, detritus, or a combination of the three in a laboratory experiment.

(2) to determine whether crayfish preferred one dietary component over the other if given equal amounts of macroinvertebrates, detritus, and algae in a laboratory experiment.

The rocky areas support a balanced, but short food web of benthic algae, crayfish, and yellow perch (*Perca flavescens* Mitchill). Results of this study will contribute to a better understanding of this food web and provide baseline data on the undisturbed benthic food web for comparison to any changes to this habitat as a result of the 1992 infestation of zebra mussels.

TABLE 1

Average gut contents (% composition biovolume) of 45 crayfish (*O. propinquus* and *O. virilis*)

Organisms found in guts	**% Composition**
Algae:	
Achnanthes minutissima	5
Cladophora sp.	12
Cymbella cistula	6
Cymbella microcephala	4
Fragilaria vaucheriae	5
Lyngbya sp.	6
Melosira distans	3
Mougeotia sp.	3
Navicula pellusida	4
Nitzschia palea	7
Nitzschia palea var. *debilis*	2
Phormidium tenue	1
Total Algae:	**58**
Invertebrates:	
Caecidotea sp.	6
Chironomid species	4
Gammarus sp.	2
Stenonema sp.	1
Unidentified parts	5
Total Invertebrates:	**18**
Detritus:	
Leaf litter	3
Maple tree samaras	1
Amorphous debris	20
Total Detritus:	**24**

Source: N.C. Tuchman, unpublished data.

Note: Crayfish were collected from southwestern Lake Michigan in May, June and July, 1989.

CHAPTER II

LITERATURE REVIEW

Lake Michigan

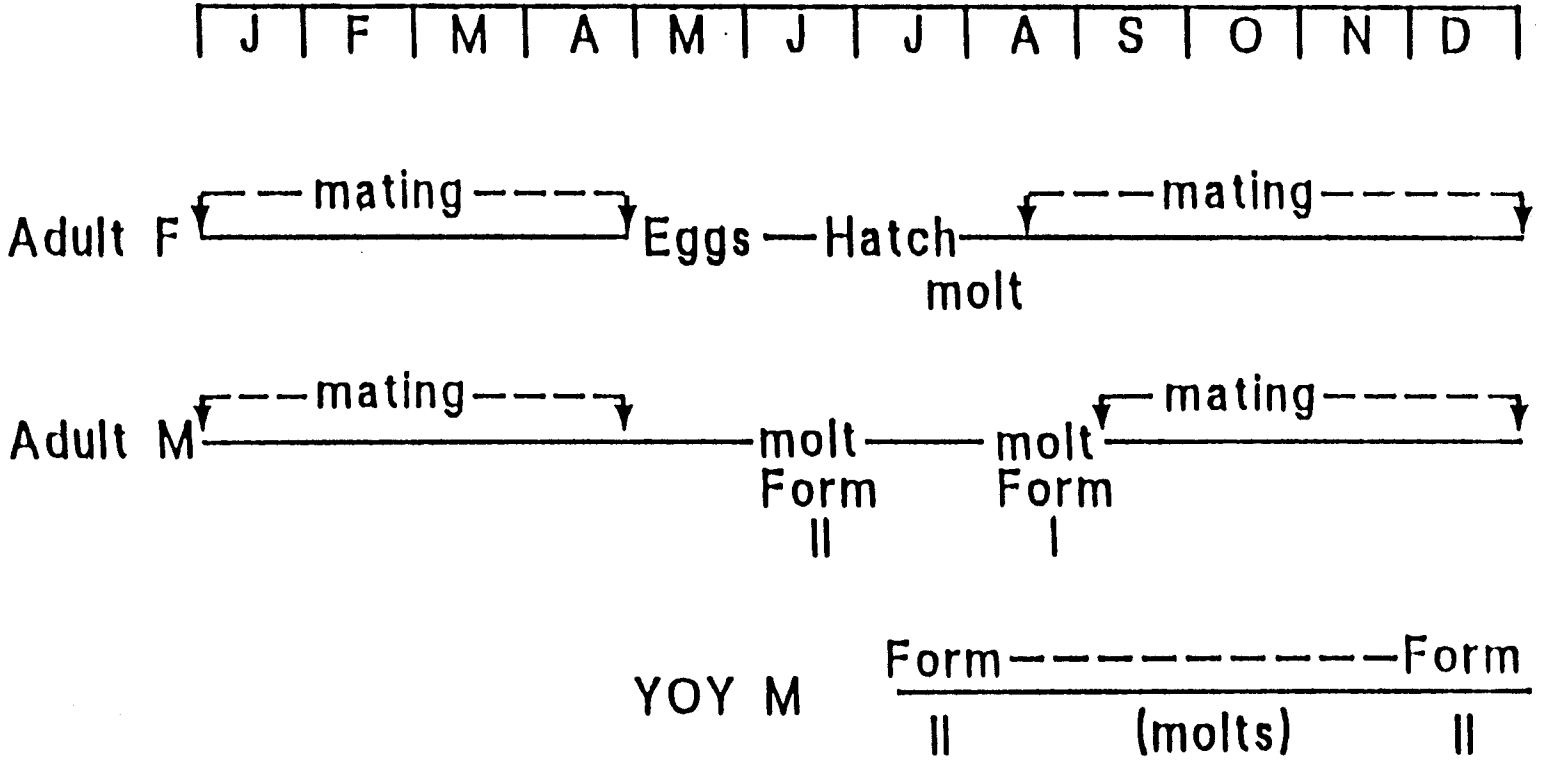
The Laurentian Great Lakes of North America constitute the greatest continuous mass of fresh water on earth with a collective area of 245,240 km^2 and a volume of 24,620 km^3 (Wetzel 1983). The retreat of the Wisconsin ice sheet approximately 15,000 years before present left what are now the contemporary Great Lakes basins (Wetzel 1983). Lake Michigan is a cold (18 - 20°C summer temperatures) deep lake (281 meters maximum) with a long hydraulic retention time (104 years) (Goldman and Horne 1983). Lesht and Rockwell (1987) qualified Lake Michigan as an oligotrophic lake based on the amount of particulate phosphorus and chlorophyll-a in the surface waters, secchi depth readings, and presence of certain blue-green algal species (indicative of oligotrophic status) in the water column. Lake Michigan receives low levels of allochthonous input as a result of its low watershed area to lake area ratio and, therefore, has low productivity. Within about 20 km of Lake Michigan's southwestern shore, the lake floor is a dynamic environment where currents induced by storm activity transport sand and fine silt resulting in a patchy,

continually changing distribution of lacustrine sediment overlying a till-gravel pavement (Folger *et al.* 1994). Exposed, natural rocky areas found in this portion of the lake provide solid substrata for the benthic community.

Crayfish

Life history. Basic life history of *O. propinquus* in different habitats has been described by several researchers including Van Deventer (1937), Capelli (1975), and Corey (1988). While the order of life history events remains the same for each of the described habitats, the timing is slightly different. Capelli found water temperature influenced the timing of molts; individuals residing at greater depths in cooler waters molted later than those in warmer, more shallow waters. The life history for crayfish in the Lake Michigan rock reefs was described by Quinn and Janssen (1989) and is summarized in Figure 1. Most female crayfish mate by October and undergo ovarian maturation during the winter months. Eggs are deposited on the female pleopods in the spring and are carried from May through June. Eggs hatch in early July and the juveniles remain attached to the female's pleopods until the middle of July. Male crayfish molt to change from Form I (breeding condition) to Form II (non-breeding condition) in early June. Most males molt back to Form I in early September and remain in this breeding form until the following June. Young-of-year crayfish molt several times during the summer and fall, continuing to grow but

Figure 1. Life history events of *O. propinquus* from Lake Michigan rock reefs (Quinn and Janssen 1989) (figure is modified from Capelli 1975).


J F M A M J J A S O N D
Adult F
mating
Eggs
Hatch
molt
mating
Adult M
mating
molt
Form
II
molt
Form
I
mating
YOY M
Form
II
(molts)
Form
II

remaining in Form II until mating in the fall of their second year.

Taylor (1990) reported that crayfish exhibit indeterminate growth, molting throughout their lives. Size increases, which vary between 2-4mm per molt (Boyd and Page 1978; Weagle and Ozburn 1978; Shimizu and Goldman 1983), are dependent upon both growth increment (growth per molt), and molt frequency (Sadewasser and Prins 1979; Thorp and Winetriter 1981; Shimizu and Goldman 1983). Some male *O. virilis* were found to molt up to three times during the summer months (Hazlett and Rittshof 1985). Van Deventer's (1937) work in central Illinois with male *O. propinquus* found that some young-of-year matured by the end of the first growing season, mated during the next season, produced young and died. In Trout Lake, Wisconsin, Capelli (1975) found that no young-of-year matured by the end of the first season and that those in Trout Lake had to survive into the third season to reproduce, attributing this difference to a shorter growing season and colder temperatures prolonging the time needed to reach maturity. Momot *et al.* (1978) cited density, temperature regime, and food availability as growth-limiting factors in crayfish populations.

Fielder (1972) reported the most common growth increment in *O. propinquus* was one to two millimeters (sometimes more) of carapace length per molt and that growth did not always accompany a form change. In Lake Michigan, young-of-year *O.*

propinquus in the fall ranged from 9mm to 15mm in carapace length while adult *O. propinquus* (male form I) were 16 to 32 mm in length (Quinn and Janssen 1989). Quinn and Janssen (1989) found that the growth rates of *O. propinquus* and *O. virilis* were similar to other populations in studies reported by France (1985), Hazlett and Rittschof (1985), and Momot *et al.* (1978).

Habitats and niches of crayfish. Crayfish, the largest freshwater crustaceans in North America, inhabit a wide variety of aquatic and semiaquatic environments (Momot 1967, Hobbs 1972, Pennak 1989). In benthic communities, crayfish feeding and reproductive behaviors can have a strong impact on the growth and feeding behaviors of other species within the community (Rickett 1974). Crayfish can act as keystone predators in lotic habitats by having both positive and negative effects on other members of the community (Hart 1992). By consuming the branched filamentous green alga, *Cladophora* spp., crayfish negatively affect invertebrate taxa whose abundances positively correlate with *Cladophora* (or positively affecting those whose abundances negatively correlate with *Cladophora*) (Hart 1992). Crayfish are capable of utilizing and occupying different trophic levels and, thus, play a complex role in the trophic interactions within aquatic ecosystems (Lorman and Mangnuson 1978).

By virtue of their interactions with all trophic levels in lakes, crayfish have the potential to influence the

structure and contribute to the stability of lake communities (Momot *et al.* 1978; Capelli 1980). Flint & Goldman (1975) found that crayfish grazing on benthic algae significantly affected rates of primary production within a lake ecosystem. At low densities, crayfish grazing enhanced benthic primary productivity, while grazing activity by higher crayfish densities drastically reduced primary production. Hanson *et al.* (1990) found that relatively low densities of crayfish could have an impact on the structure of the macroinvertebrate communities of lakes by greatly reducing snail densities via predation.

Momot *et al.* (1978) suggest that in lakes where benthic algae are of greater importance than phytoplankton, the crayfish become increasingly more influential in the process of energy turnover, and material transfer up the trophic cascade. Studies of crayfish physiology indicate that nutrient uptake on the cellular level is very rapid (Speck and Urich 1970), thus in ecosystems where phytoplankton production is low, crayfish could be more important to the process of energy cycling, turnover, and material transfer than other microcrustaceans (Momot et al. 1978). In addition to exploiting the benthos, crayfish constitute a pathway for converting detritus, especially allochthonous leaf material, into secondary production (Mason 1963). Orzechowski (1973) demonstrated that assimilation efficiencies of *Orconectes limosus* were as high as 46%, allowing these organisms to

convert about 9% of the inflowing energy of a benthic system (assumed to be macrophytes) into secondary biomass in 24 hours. In the nearshore waters of southwestern Lake Michigan, it is likely that crayfish, already the dominant macroinvertebrate, will become increasingly more important as an energy link between benthic algae and yellow perch since the zebra mussels have caused a shift from a phytoplankton-based to a benthic filamentous algal-based system.

Generally, crayfish are considered to be omnivorous with some species displaying varying food preferences with age (Creaser 1934; Abrahamsson 1966; Miller & Van Hyning 1970; Mason 1975; Capelli 1980). Gut contents of crayfish from a marl lake ecosystem were found to contain green algae, vascular plant fragments and other miscellaneous organisms, indicating the crayfish to be primarily herbivorous and also facultative scavengers (Momot 1967). Capelli (1980) found that in Trout Lake, Wisconsin, crayfish fed on not only algae, but also midge larvae, mayfly nymphs, and other crayfish with cannibalism attributed to adults preying upon newly hatched young in shallow waters. Detritus, in the form of allochthonous leaf litter, and submerged aquatic macrophytes comprises a large component of the diet of *Orconectes rusticus rusticus* Girard (Prins 1968). Particulate detritus, as a food resource, supports (directly or indirectly) over half the animal production in most ecosystems (Bowen 1987). In general, adult crayfish feed more extensively on plant

material and detritus and rely less on animal biomass for sustenance (Abrahamsson 1966; Dean 1969; Lodge & Lorman 1987) while juveniles feed largely on animal material (Momot *et al.* 1978). Vannote (1963) found that young-of-year *O. propinquus* ate 40% animal material, 30% filamentous algae, 20% plant fragments, and 10% detritus. Similarly, guts of juvenile crayfish contained chironomid larvae, cladocerans, ostracods, small dragonfly naiads, chironomid eggs, and chitinous fragments from the shells of arthropods (including crayfish) (Momot *et al.* 1978).

In laboratory studies where crayfish were fed only periphytic algae, filamentous algae appeared to be preferred over other algal growth forms. Bert (unpublished, 1990) observed crayfish selectively feeding on large green filamentous algae (*Mougeotia* sp.), leaving single-celled attached diatoms unaffected. Similarly, laboratory experiments conducted by Zenchak (1993) revealed that crayfish selectively fed on algal taxa that were prevalent in the canopy of benthic algal communities. *Orconectes virilis* showed distinct feeding preferences when allowed to feed *ad libitum* for 48 hours on ten commonly occurring species of aquatic macrophytes (Chambers *et al.* 1991). *Orconectes rusticus* and *Procambarus clarkii* avoided macroalgae and macrophytes with structural or chemical deterrents, showing a preference for plants high in nitrogen (Lodge and Cronin 1994). In general, species of *Orconectes* graze macrophytes

selectively in both the laboratory and the field (Seroll and Coler 1975; Lorman 1980; Lodge and Lorman 1987; Lodge 1991; Olsen *et al*. 1991). Capelli (1980) found that crayfish diet not only changed seasonally, but apparently varied as a result of selective feeding. In laboratory experiments crayfish preferred eggs of lake trout (*Salvelinus namaycush*), whitefish (*Coregonus clupeaformis*), and walleye (*Stizostedion vitreum*) to algae and other common food items.

Crayfish secondary production, defined by Teal (1957), as "the amount of energy available to the next trophic level, and the ratio of this energy (net production) to total assimilation indicates the efficiency with which energy is fixed in body tissues of members of a population and made potentially available to other trophic levels," differs depending on food sources. In laboratory experiments, Moshiri and Goldman (1969) demonstrated that although plant-fed *Pacifastacus lenuisculus* (Dana) had lower assimilation efficiencies than those on an animal diet, they compensated by ingesting more plant material per unit time. Assimilation efficiencies in crayfish and other arthropod species have been reported by several other researchers. Suschenya (1970) showed that food conversion efficiencies differed for different species, food types, and temperatures. For example, *Daphnia pulex*, assimilates the unicellular green alga, *Chlamydomonas*, with an efficiency of 7-24%, while the isopod, *Caecidotea aquaticus*, which eats microbially conditioned tree

leaves, has an assimilation efficiency of 68%.

Defining the daily activity patterns of crayfish is important in understanding crayfish feeding behavior. Many suggest that crayfish conceal themselves by day and are active during the night. Roberts (1944) found that the feeding activity of *O. virilis* reached a maximum in the hour immediatley after the onset of darkness and declined steadily thereafter until the early hours of morning. Van Deventer (1937) observed *O. propinquus* individuals feeding during both day and night, as did Hay (1919), and concluded that this species displayed no nocturnal pattern in activity. Capelli (1975), however, found that overall activity of *O. propinquus* increased through the night with much of the activity being food-related. Quinn and Janssen (1989) found that in Lake Michigan, both *O. propinquus* and *O. virilis* left their shelters at night (approximately 30 minutes after sunset) and competed for rock shelters at dawn. Likewise, in Lake Kathleen (Emmet County, Michigan), very few crayfish (*O. propinquus* or *O. virilis*) were observed in the daylight hours while vast numbers of these species were seen leaving their shelters approximately one half hour after sunset (personal observations).

Crayfish in southwestern Lake Michigan. The rocky areas of the southwestern Lake Michigan littoral zone are inhabited by a high biomass of two species of crayfish, *Orconectes virilis* and *O. propinquus* (Janssen and Quinn 1985). These

areas support crayfish populations that subsist on limited food availability as macrophytes are absent and other macroinvertebrates and detritus are scarcely present (Zenchak 1993). Midges (Chironomidae), amphipods (*Gammarus*), Isopods (*Caecidotea*), mayflies (*Stenonema*) and caddisflies (*Psychomyia*), present in lower numbers, are the most abundant non-crayfish invertebrates of the rocky areas of Lake Michigan (Janssen and Quinn 1985). While allochthonous leaf litter has been found to enhance crayfish production in smaller lakes (Jones and Momot 1981), the input of allochthonous detritus to Southwestern Lake Michigan is likely too minimal to sustain such high crayfish populations (Janssen and Quinn 1985). Further, crayfish herbivory plays a key role in keeping the benthic algal community in a highly productive state by decreasing interspecific competition within the algal community for limiting factors such as light and nutrients (Zenchak 1993).

Gut content analyses of 45 juvenile and adult crayfish (*O. propinquus* and *O. virilis*), collected from southwestern Lake Michigan in 1989, revealed that, regardless of crayfish age, algae comprised the largest percent of gut content biovolume while detritus and macroinvertebrates totalled 24 and 18 percent, respectively (Table 1). Crayfish, the primary prey of the local yellow perch (*Perca flavescens*) (Abrant 1988), in turn, comprised 90% of the perch diet in the late summer months on the rock areas. These data suggest that

benthic algae are the most important food source to both juvenile and adult crayfish in this habitat and that crayfish are an energetically important link between algae and the top carnivore, yellow perch, as densities of other macroinvertebrates are extremely low (Zenchak 1993).

CHAPTER III

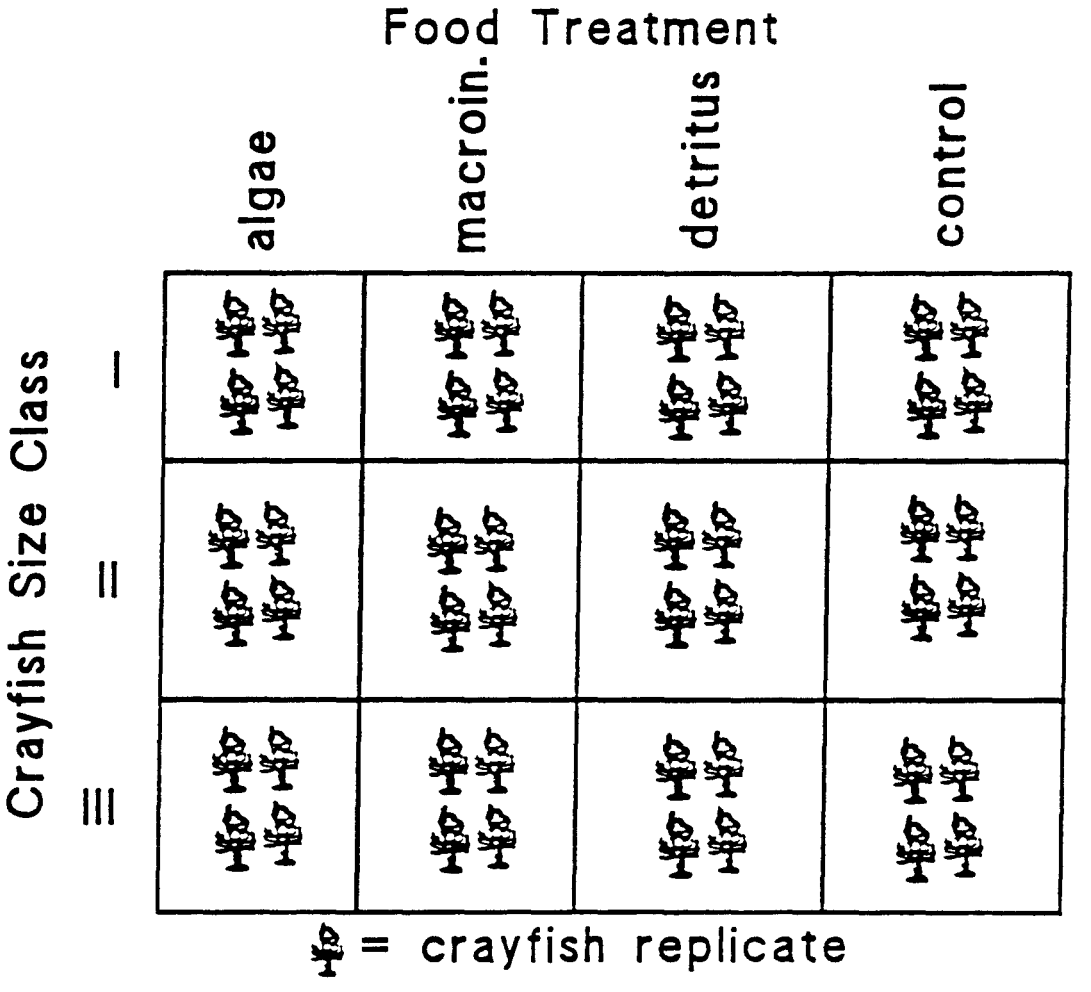
MATERIALS AND METHODS

Growth Rate Study

During the summer and fall months of 1991, a laboratory study was conducted in order to assess growth rates of male *O. propinquus* reared on different diets. Four food treatments, including benthic algae, detritus (microbially conditioned allochthonous leaf litter), macroinvertebrates and a control (combination of algae, detritus and macroinvertebrates) were established for each of three size classes of *O. propinquus*. The 4 x 3 design was replicated four times as depicted in Figure 2.

Treatments. A source of algae for use in this study was established, by methods of Zenchak (1993), as follows. Benthic algae was collected by taking rocks from the Lake Michigan rock site and bringing them back to the laboratory where algae was scraped from them using a stiff bristle brush. The algal slurry was placed in two circulating pools in the laboratory (0.9m diameter; volume=108.2 L dechlorinated water; water current established by submersible pump). Water temperatures in the pools were maintained between 15°C and 17°C and illuminated by four, 40-watt wide spectrum bulbs

Figure 2. Diagram of the growth rate study design assessing growth of individual crayfish, fed on one of four diets, by size class and food treatments.


Food Treatment
algae
macroin.
detritus
control
Crayfish Size Class
I
II
III
= crayfish replicate

simulating a 14 hour photoperiod. Nutrients (Guillard's F_1 algal media) (James, 1978) were added to the pools to stimulate algal growth. Unglazed clay tiles (area of each tile = 24.01cm^2) lined the bottom of the pools serving as substrata for algal colonization.

An organophosphorus insecticide, temephos, ("Abate"; Clark Outdoor Spraying, Roselle, IL) was added to the algal colonization pools, following the protocol described by Yasuno *et al.* (1985), to prevent contamination of the algal food source by chironomid larvae. This treatment was added only once, on the same day the algal slurry was introduced to the pools. Temephos had no measurable effect on algal biomass. The tiles supported a benthic algal thickness averaging 3 cm to 5 cm and were dominated by filamentous green algae (*Cladophora* spp. and *Mougeotia* spp.), filamentous blue-green algae (*Phormidium tenue* and *Oscillatoria* sp.), as well as various species of diatoms. Approximately four weeks was needed to produce substantial algal biomass on the tiles.

Neither detritus nor macroinvertebrates could be collected in adequate amounts from the Lake Michigan rock reef to provide saturated quantities for the crayfish throughout the study. Thus, these food items were obtained from other sources. The detritus (microbially conditioned and crushed leaf litter >1.0mm diameter) was collected from the sediment surface of a nearby pond and rinsed free of macroinvertebrates. The macroinvertebrate food treatment

consisted of fly and beetle larvae (Diptera spp. and *Tenebrio molitor*) obtained from a local bait shop, supplemented by diced lake perch when fly and beetle larvae were not available in large enough quantities.

Crayfish collection. Lake Michigan light levels and water temperatures were measured *in situ* and replicated in the Loyola University greenhouse. A LiCor Quantum Photometer and a YSI thermister were used to obtain light levels and water temperature readings from the crayfish collection site in Lake Michigan. Water temperature (mean water temperature = 14.4 °C) and light levels (mean Photosynthetically Active Radiation value at the sediment/water interface = 192.2 μmol m^{-2} sec^{-1}) from this site were reproduced in the laboratory for algal colonization and the crayfish growth rate experiment.

Crayfish were collected from approximately 6.5 m depth at the rocky area of the southwestern Lake Michigan littoral zone used by Zenchak (1993), located approximately 1 km offshore from Touhy Avenue, Chicago, Illinois. This site supported benthic algae and served as habitat for populations of *O. propinquus* and *O. virilis*.

Between June 13 and June 18, 1991, male *O. propinquus*, were collected by hand (using SCUBA) at a depth of 6.4 m on the rocky bottom of the littoral zone. Crayfish were categorized into three size classes based on carapace length: I (19.9-28.8mm total body length, 0.19-0.64g wet weight body mass age: young-of-year), II (15.5-18.3mm carapace length,

1.28-2.51g ww), III (21.0-26.5mm carapace length, 3.36-7.15 g ww). Carapace length of young-of-year crayfish was difficult to measure, so total body length was used since carapace length in *O. propinquus* is nearly one-half the total length for all size classes of crayish (Capelli 1975). Crayfish were returned to the Loyola University greenhouse where experiments were conducted in large plastic tanks.

Each tank (dimensions = 0.46m x 0.35m x 0.33m) housed one individual crayfish and was filled with approximately 50 L of dechlorinated tap water that was continually aerated throughout the study. A Lake Michigan rock (scrubbed and autoclaved to remove all attached organic material which could potentially serve as crayfish food) was placed in each tank for crayfish shelter. All tanks were maintained in a laboratory greenhouse under simulated Lake Michigan conditions (chamber light levels = 72 μmol m^{-2} sec^{-1}; chamber water temperature = 13°C - 17°C). The greenhouse was subject to natural diel changes in light; crayfish tanks were shaded with cotton cloth to attain the light conditions similar to those at the Lake Michigan collection site. Temperatures in the greenhouse were controlled with air conditioning units and monitored with maximum/minimum thermometers.

Sampling. To assure ample time for the assessment of crayfish growth, this laboratory experiment ran for 61 days. During this time, food, of the appropriate type, was continually supplied *ad libitum* and wet weight and carapace

length for each individual crayfish were recorded every five days. Orzechowski (1973) showed that *Orconectes limosus* consumed an average of 50% of their body weight per day, with small crayfish consuming 7%. For this experiment, saturation levels of each food type were maintained throughout the experiment by giving each crayfish 0.5 grams (wet weight) of food per gram of crayfish wet body weight, every 5 days. Surplus food was always found in all tanks when new food was added. A Fisher Scientific top loading balance was used to weigh crayfish and food. Crayfish were blotted dry using a cotton cloth to remove excess water and then placed in a pre-weighed 250ml beaker of water for wet weight measurement. Placing the crayfish in a beaker of water reduced the activity of the crayfish during weighing and allowed for a more accurate reading from the scale. Water in the crayfish tanks was changed every three to five days to remove feces and excess algal, bacterial, and fungal growth (possible confounding food sources). After 61 days, growth rates were calculated for all crayfish in each size class and food treatment and the overall interaction of size class and food treatment on growth rates was determined.

Dietary Preference Study

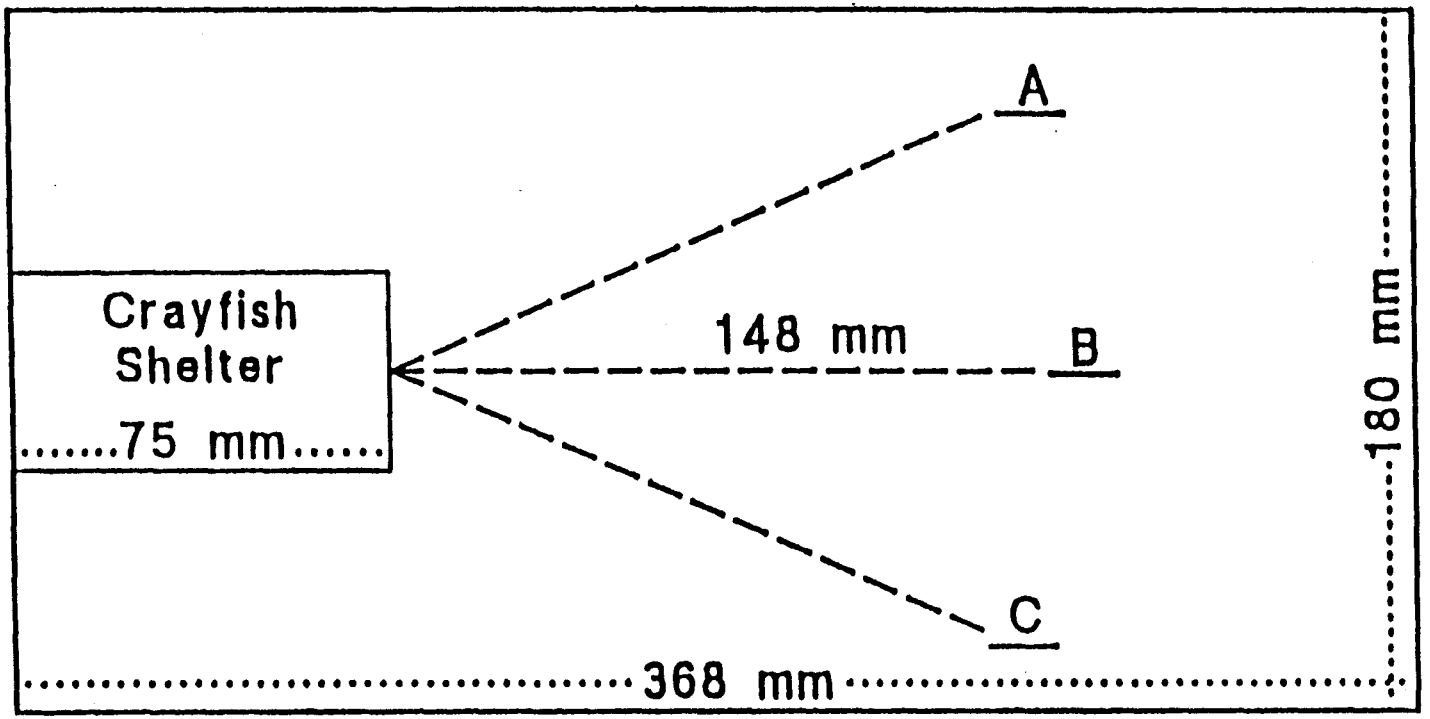
A study was conducted to determine whether crayfish fed selectively when given equal access to algae, macroinvertebrates and detritus. Because it was not possible to collect necessary quantities of all major dietary components available

to crayfish in their Lake Michigan habitat, this study was conducted at the University of Michigan Biological Station (Emmet County, Michigan) where crayfish and their food sources were readily available in vast quantities from nearby undisturbed lakes and streams.

Fifty male *O. propinquus* were collected by hand from the littoral zone of Lake Kathleen (Emmet County, Michigan). The crayfish ranged in size from 1.1 - 9.5 g wet weight. Macroinvertebrates including *Stenonema* (Ephemeroptera), *Hydropsyche* (Trichoptera) larvae, *Glossosoma* (Trichoptera) and *Neophylax* (Trichoptera) (with cases), Chironomidae, and small Perlidae were collected by hand from submersed rocks in the East Branch of the Maple River. These macroinvertebrates represented a faunal assemblage and taxa similar to those found in Lake Michigan. Using plant grapples, samples of filamentous green algae including, *Cladophora, Spirogyra,* and *Mougeotia* were collected from the littoral zone of Douglas Lake. Microbially conditioned allochthonous leaf litter (*Acer* spp. and *Quercus* spp.) was collected by hand from the littoral zone of Douglas Lake. The algae and leaf litter represented taxa that can be found in southwestern Lake Michigan.

Experimental Tanks. Fourteen 25-gallon experimental tanks were constructed, each bearing three marked locations on the tank bottom for placement of the three food types (Figure 3). Each mark was equidistant from the center of the entrance to a crayfish shelter fashioned from PVC pipe (7.5 cm long,

Figure 3. Top-down view of the bottom of the experimental tanks designed for the preferential feeding study. A, B, and C denote sites for random placement of food components.


A
Crayfish
Shelter
75 mm
148 mm
B
180 mm
C
368 mm

5.0 cm diameter, cut in half lengthwise) (Figure 3). The experimental tanks were filled with water from Douglas Lake, aerated with an air stone. All sides of the experimental tanks were covered with black mesh shade cloth to provide a more enclosed shelter and minimize stress for the crayfish. All tanks housed at the UMBS outdoor research facility were subject to diel changes in light. Crayfish were acclimated to their tanks for 2 days prior to the start of the preferential feeding experiments.

Crayfish. Crayfish for the experiments were collected over a period of four nights after 2230 EDT when crayfish were observed to be most active and, therefore, were easiest to collect in Lake Kathleen. On each of the collection nights, fifteen to twenty male crayfish were collected and, upon return to the laboratory, immediately placed individually in experimental tanks. Those not used in experimental tanks were placed in one of three 50 gallon holding tanks. One of the tanks held "extra" crayfish from collections and the other two tanks housed those used after experimental trials were run so that crayfish could not be retested. Crayfish were starved for 24 hours prior to the start of each experiment.

Sample Preparations. To test whether the crayfish preferred one or more of the dietary components, individually starved crayfish were offered equal biovolumes (0.5 ml) of each of the three food types (algae, macroinvertebrates and detritus). The detritus was blotted dry on paper tissues and

measured using volume displacement in a graduated cylinder. The filamentous green algae was first placed in a white enamel pan of water and macroinvertebrates and large particulate detritus was removed using forceps. The algae was then blotted dry on paper tissues and measured using volume displacement in a graduated cylinder. The rocks, to which macroinvertebrates were attached, were placed in enamel pans with water. Using forceps, the macroinvertebrates were gently removed from their cases or crevaces and placed in graduated cylinders for measurement by volume displacement.

Experimental trials. Forty-three crayfish were observed in four experimental trials conducted over the course of four nights. Each trial began in natural darkness, after 2230 EDT, in keeping with the crayfish activity pattern observed in Lake Kathleen. Artificial red lights were used to minimize crayfish stress and provide adequate light to observe crayfish feeding activity (Tierney and Atema 1988). A random numbers table (Remington and Schork 1985) was used to determine the location of each food type within each experimental tank (Figure 3). Only one tank was observed at a time for each experimental observation. Prior to the start of each observation, the crayfish was encouraged into its shelter using a glass rod. Using forceps, 0.5 ml of each food type was then placed into the tank at the three designated locations equidistant from the entrance to the shelter. The crayfish was then observed for ten minutes, during which the

amount of time spent handling (including manipulating or ingesting) each food type was documented using three simultaneous stopwatches (one watch for each food type). Because it was usually impossible to discern whether a crayfish was ingesting or merely manipulating food, "handling time" (any manipulating, ingesting or crayfish contact with the food) was measured as an indication of preference for food type. Upon the completion of all ten-minute observations, the crayfish were removed from the experimental tanks and transferred to a holding tank. The experimental tanks were then washed and refilled in preparation for the next night's trial.

Diel observation. To test whether what the crayfish preferred to manipulate or ingest in the ten minute observations was indicative of what they ingested over a longer period, a study was conducted in which five individual crayfish were observed for 24 hours. The methods for this study were similar to those employed in the preferential feeding study. Each crayfish was placed in a separate experimental tank and starved for 24 hours. To ensure satiation levels of food, equal biovolumes (5.0 ml) of food were introduced to the tanks. For this study, macrophytes (*Elodea*) were included as a food treatment in addition to the algae, macroinvertebrates and detritus. Though macrophytes are unavailable as a dietary component to crayfish in Lake Michigan, they are prevalent in Lake Kathleen.

Crayfish activity was documented for ten minutes every 2 hours for the first three observation periods, and thereafter, every 6 hours for a total of 24 hours. During each observation period, an assessment of food components remaining in each experimental tank was made by counting remaining macroinvertebrates and visually estimating remaining quantities of the other food types. After 24 hours, crayfish were removed from the tanks and all remaining macrophytes, macroinvertebrates, filamentous algae and detrital particles large enough to be handled with forceps were removed and blotted dry with tissue papers. Biovolume of material from each category was estimated in a graduated cylinder using volume displacement. The remaining water was filtered using a 0.45μm Millipore filter to measure all additional algal filaments that had become suspended in the water column.

Problems were encountered in trying to recover and separate all of the algae from the detritus on the filter papers. Final measurements of algal and detrital biovolumes are rough estimates because of difficulty in separating and completely sampling each food component. There was also the possibility that some of this material was ingested by macroinvertebrates during the 24 hour trial. While most of the macroinvertebrates used in the study were omnivorous, Hydropsychidae were predominantly herbivorous, known to feed on diatoms, other algae and higher plants (Pennak 1953).

Statistical Analyses

Growth rate study. A two-way analysis of variance was conducted to determine what effect size class and dietary treatment had on adult crayfish growth (size classes II and III) (Zar 1984; Systat 1989). Young-of-year crayfish growth was assessed with an analysis of variance (due to their different molt cycle they were not included in the two-way analysis with the adult crayfish). This was followed by a Tukey-type multiple comparison test to determine which treatments significantly differed (Zar 1984). Percent weight change, used to evaluate crayfish growth, was defined as:

$$\text{Percent weight change} = \frac{\text{Weight}_{\text{final}} - \text{Weight}_{\text{initial}}}{\text{Weight}_{\text{initial}}} \times 100$$

where initial weights were crayfish weights recorded on day 1 of the experiment and final weights were those recorded on day 61.

Dietary preference study. A nonparametric Friedman rank test was used to assess homogeneity of handling times of food treatments within each of the four experimental trials conducted, such that time spent not handling any food was also taken into account. The null hypothesis test of this analysis was: time handling algae = time handling macroinvertebrates = time handling detritus = time handling no food (Zar 1984). This was followed by a Tukey-type multiple comparison application for ranked data in a randomized block to determine between which food types a difference in handling time occurred (Zar 1984).

A modification of Strauss' Linear Food Selection Index (Strauss 1979) was used to determine preference for, or avoidance of, specific food types in the dietary preference study:

$$P_i = t_i - a_i$$

where t_i is the proportion of time spent handling a specific food type (out of the total time spent handling any food type), and a_i is the proportion of total food available that i represents (in all cases, $a_i = 0.333$). The food groups were thus designated as:

(1) P_a = proportion of time spent handling algae (out of total time spent handling any food type) - 0.333

(2) P_m = proportion of time spent handling macroinvertebrates (out of total time spent handling any food type) - 0.333

(3) P_d = proportion of time spent handling detritus (out of total time spent handling any food type) - 0.333

P_i values, therefore, could range between 0.666 and -0.333 with positive values indicating preference and negative values indicating avoidance. The absolute value of P indicated the degree of preference or avoidance for that given food type.

A two-way analysis of variance was conducted to determine whether size class and food type had an effect on P values (Mystat 1992). This was followed by a Tukey test to determine

which treatments differed significantly from one another.

CHAPTER IV

RESULTS

Growth Rate Study

An effect of dietary treatment on crayfish growth was found for size class I crayfish (ANOVA; $p<0.011$)(Table 2). No significant effect of food treatment or size class on crayfish growth was detected for size classes II and III (Table 3). While size class I crayfish increased up to 110% over the 61 days, size class II only grew an average of 10.3% of their body weight and size class III decreased in size by an average of 4.7% (Table 4).

Size class I crayfish (YOY) were the only group to sustain positive percent weight change with all food treatments (Figure 4). Within size class I, crayfish that were fed strictly macroinvertebrates increased in weight 110 percent; significantly higher than crayfish fed algae (Tukey Test; $(0.025<p<0.05)$ or detritus (Tukey Test; $0.025<p<0.05$) (Figure 4). Crayfish given the combination diet showed a weight increase of 91 percent, which was also significantly different from the algae (Tukey test; $p<0.05$) and detritus (Tukey test; $p<0.05$) treatments, but not the macroinvertebrate treatment (Figure 4).

Size class II crayfish exhibited positive percent weight

TABLE 2

ANOVA Table for assessing the effect of dietary treatment on size class I crayfish growth

Source	df	SS	MS	F	P
Treat	3	24359.152	8119.717	6.760	0.011
Error	9	10809.797	1201.089		

TABLE 3

ANOVA Table for assessing the effect of size class and dietary treatment on crayfish growth in size classes II and III

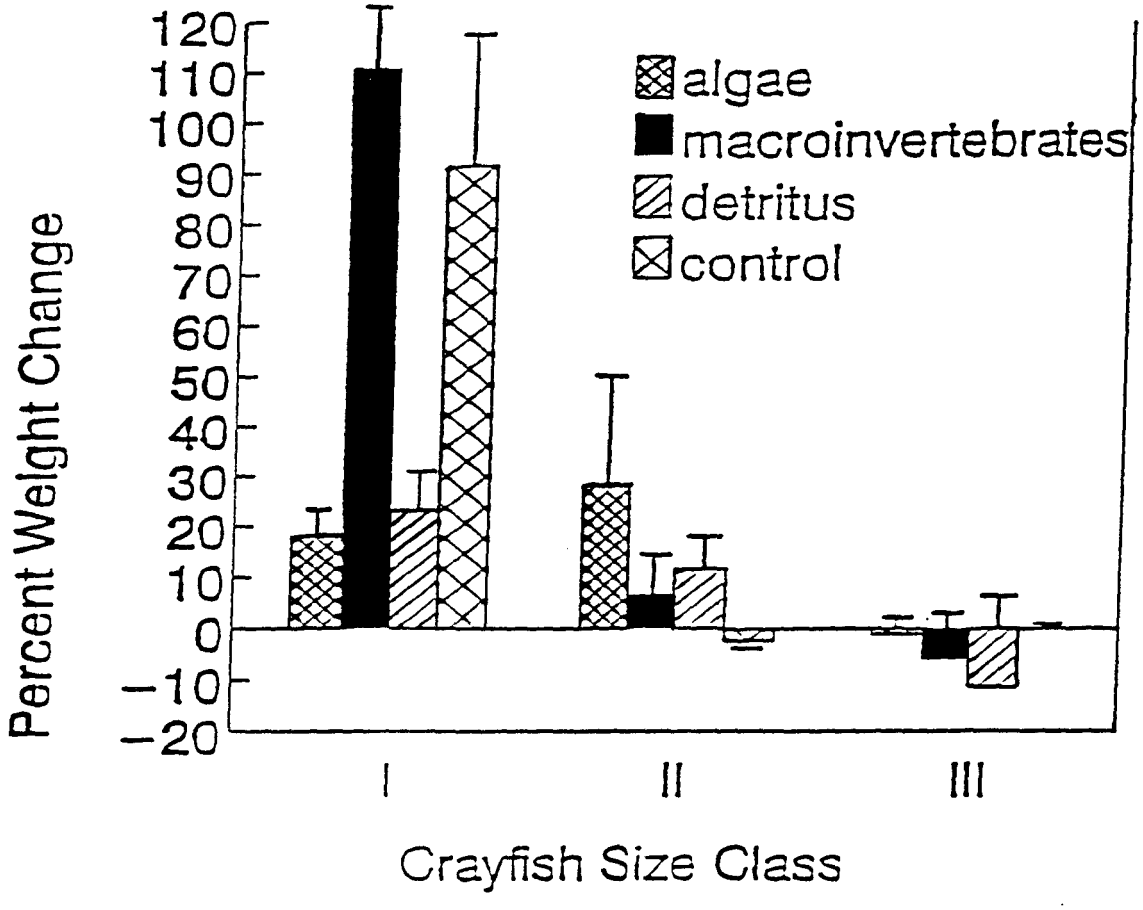
Source	df	SS	MS	F	P
Class	1	710.268	710.268	2.473	0.134
Treat	3	42.513	14.171	0.049	0.985
Class* Treat	3	469.875	156.625	0.545	0.658
Error	17	4881.683	287.158		

TABLE 4

Relative growth (percent weight change) of 3 size classes of crayfish fed experimental diets

Crayfish size class	Experimental Diets			
	Algae	Macroinvert.	Detritus	Control
I (YOY)	+17.87	+110.45	+23.23	+91.34
II (1 yr)	+25.64	+6.27	+11.72	-2.41
III (>2 yr)	-1.12	-5.92	-11.62	-0.07

Figure 4. Growth of *O. propinquus* as percent weight change per size class (+ 1 s.d.) over 61 days on four dietary treatments.


120
110
100
90
80
70
60
50
40
30
20
10
0
−10
−20
Percent Weight Change
algae
macroinvertebrates
detritus
control
I
II
III
Crayfish Size Class

changes in all food treatments except the combination treatment (percent weight change = -2.41), which was not significantly different from zero (Figure 4). No significant effect of food treatment on mean percent weight change of size class II individuals was detected. While crayfish in this size class essentially maintained their weight, an increase in variation after day 40 of the experiment (Figure 5F) was attributed to a crayfish that molted between days 36 and 41, resulting in a boost in weight (Figure 6F).

Size class III crayfish essentially maintained their weight throughout the 61 day experiment (Figure 4) with no significant differences detected among food treatments.

Dietary Preference Study

Each of the four experimental trials conducted to determine whether crayfish exhibited equal handling time of food was assessed separately. Within each trial, significant differences in handling times of different food types were detected for the experimental crayfish (Friedman's test; trial 1, $0.01<p<0.025$; trial 2, $0.0005<p<0.005$; trial 3, $0.025<p<0.05$; trial 4, $0.025<p<0.05$) (Figure 7).

On average, of the total time spent handling food, crayfish spent 3.5 times longer handling macroinvertebrates than either detritus or algae in all trials; a difference that was significant in trials 1 (Tukey test; $0.025<p<0.05$), 2 (Tukey test; $0.01<p<0.025$) and 4 (Tukey test; $0.025<p<0.05$) (Figure 7). While macroinvertebrates were also handled longer

Figure 5. Average growth of three size classes of *O. propinquus* over 61 days for each food treatment (± SEM, n = 4).

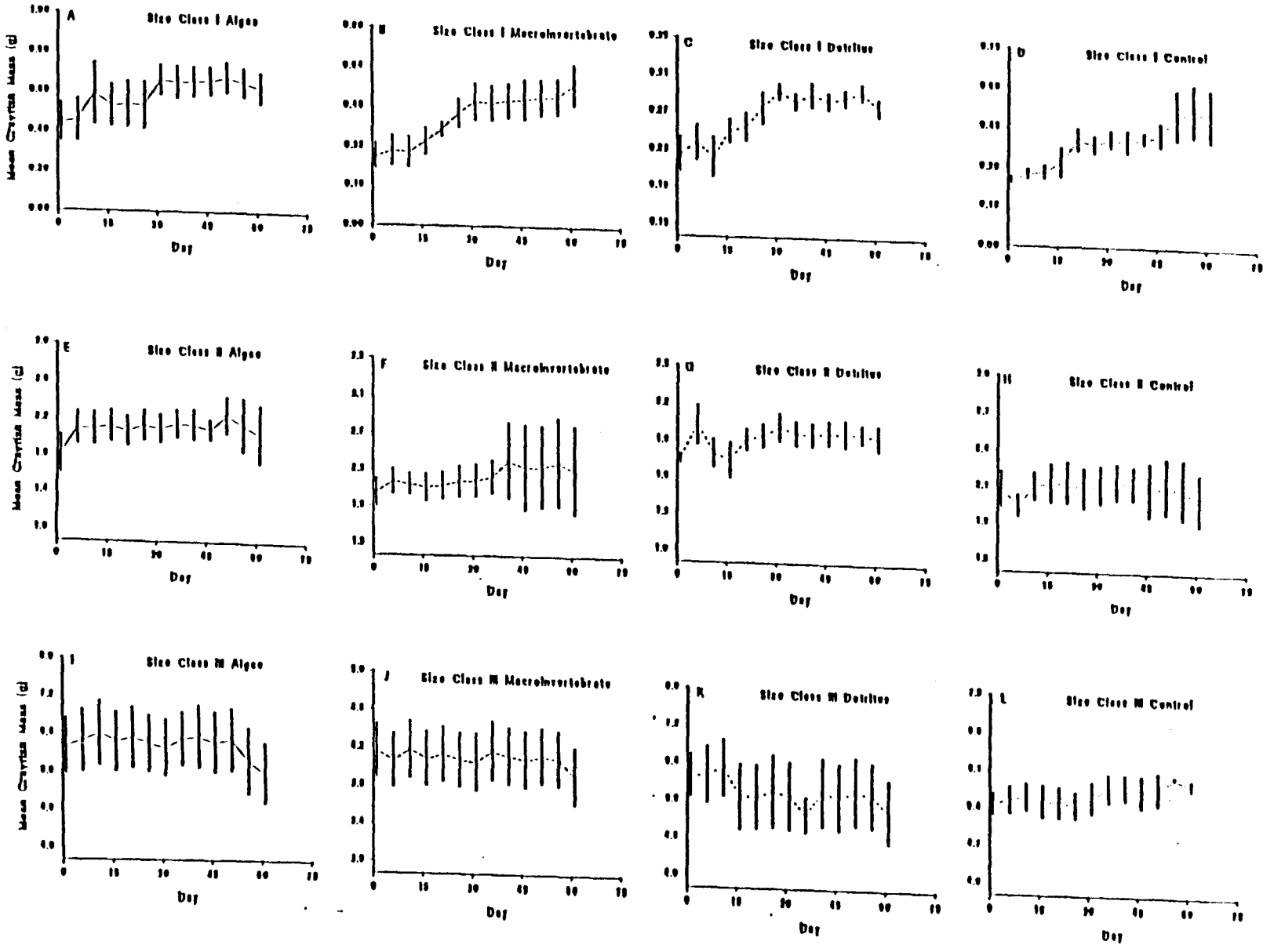

A
Size Class I Algae
B
Size Class I Macroinvertebrate
C
Size Class I Detritus
D
Size Class I Control
E
Size Class II Algae
F
Size Class II Macroinvertebrate
G
Size Class II Detritus
H
Size Class II Control
I
Size Class III Algae
J
Size Class III Macroinvertebrate
K
Size Class III Detritus
L
Size Class III Control
Mean Crayfish Mass (g)
Day

Figure 6. Average growth of individual *O. propinquus* of three size classes over 61 days within each food treatment of the growth rate study.

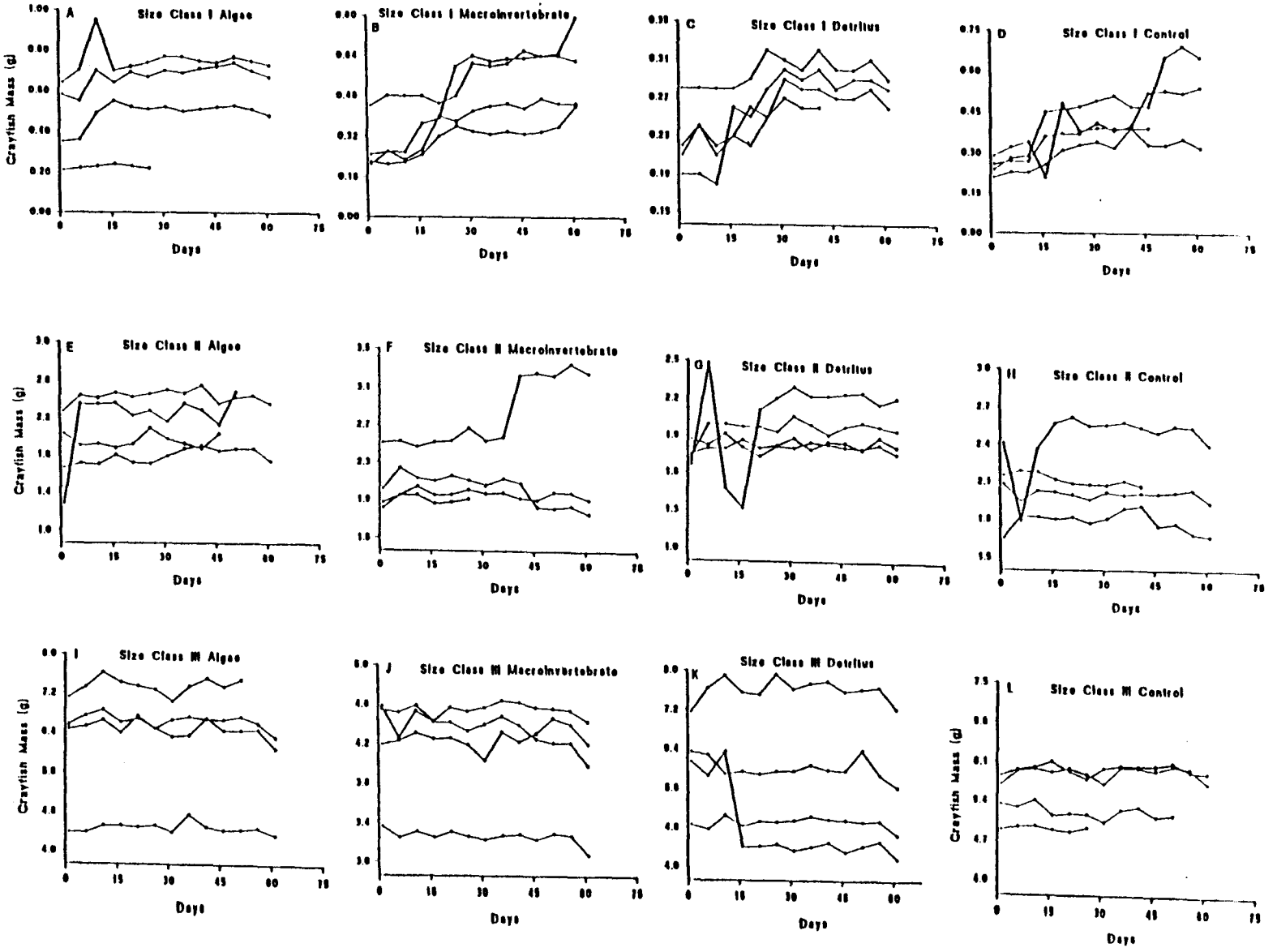
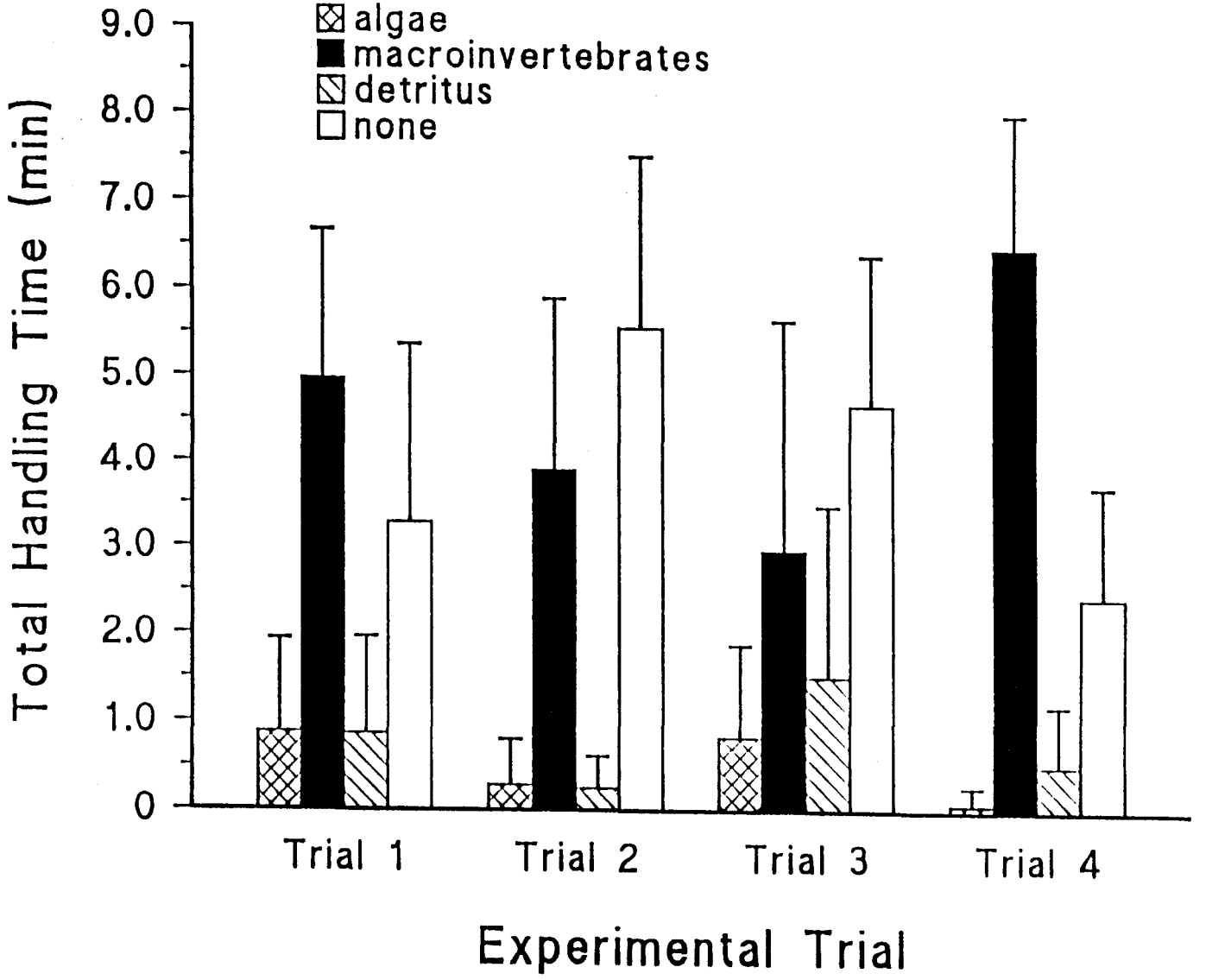

A
Size Class I Algae
B
Size Class I Macroinvertebrate
C
Size Class I Detritus
D
Size Class I Control
E
Size Class II Algae
F
Size Class II Macroinvertebrate
G
Size Class II Detritus
H
Size Class II Control
I
Size Class III Algae
J
Size Class III Macroinvertebrate
K
Size Class III Detritus
L
Size Class III Control
Crayfish Mass (g)
Days

Figure 7. Total time (minutes) crayfish handled dietary components for each experimental trial (± 1 s.d.) within the dietary preference study.


algae
macroinvertebrates
detritus
none
Total Handling Time (min)
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0
Trial 1
Trial 2
Trial 3
Trial 4
Experimental Trial

in trial 3, the difference was not significant (Tukey test; $0.05<p<0.10$) (Figure 7).

Food preferences of individual crayfish, as determined by the selective feeding index are depicted in Figure 8. Index values for the three food types differed significantly (ANOVA; $p<0.001$) with P_m value ($x = 0.39$) > mean P_d value ($x = -0.18$) > mean P_a value ($x = -0.22$). These results indicate a strong preference for macroinvertebrates, over detritus or algae. When preference indices were compared against crayfish size class, it was apparent that the food preference was unrelated to size class (Figure 8).

24-hour preferential feeding study

The results of the 24 hour preferential feeding study support results from the short-term feeding experiment suggesting that crayfish prefer to feed on macroinvertebrates when given equal access to different dietary components. As discussed in the previous section, due to the problems of recovering and separating all food particles from the tank water, only estimates of the food remaining in the tanks were made. Most of the food particles (approximately >95% biomass), however, were recovered and separated from one another giving a useful assessment of the percent of food remaining in the experimental tanks. During the 24 hours of feeding, *O. propinquus* consumed 69% of the macroinvertebrates as opposed to only 35% of the algae, 12% of the macrophytes, and 5% of the detritus (Figure 9). The slight increase in the

Figure 8. Preference index scores per weight of individual crayfish in dietary preference study.

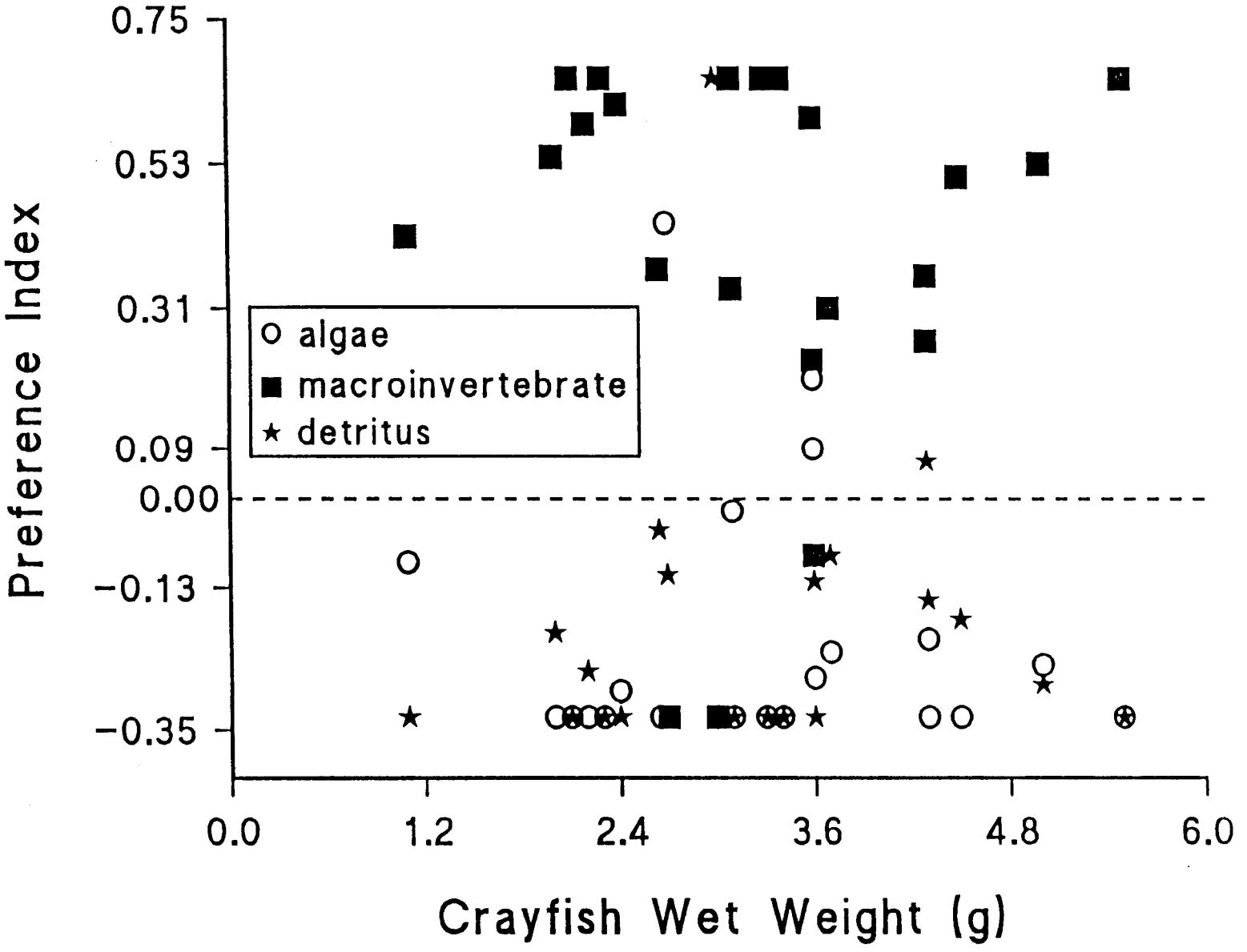
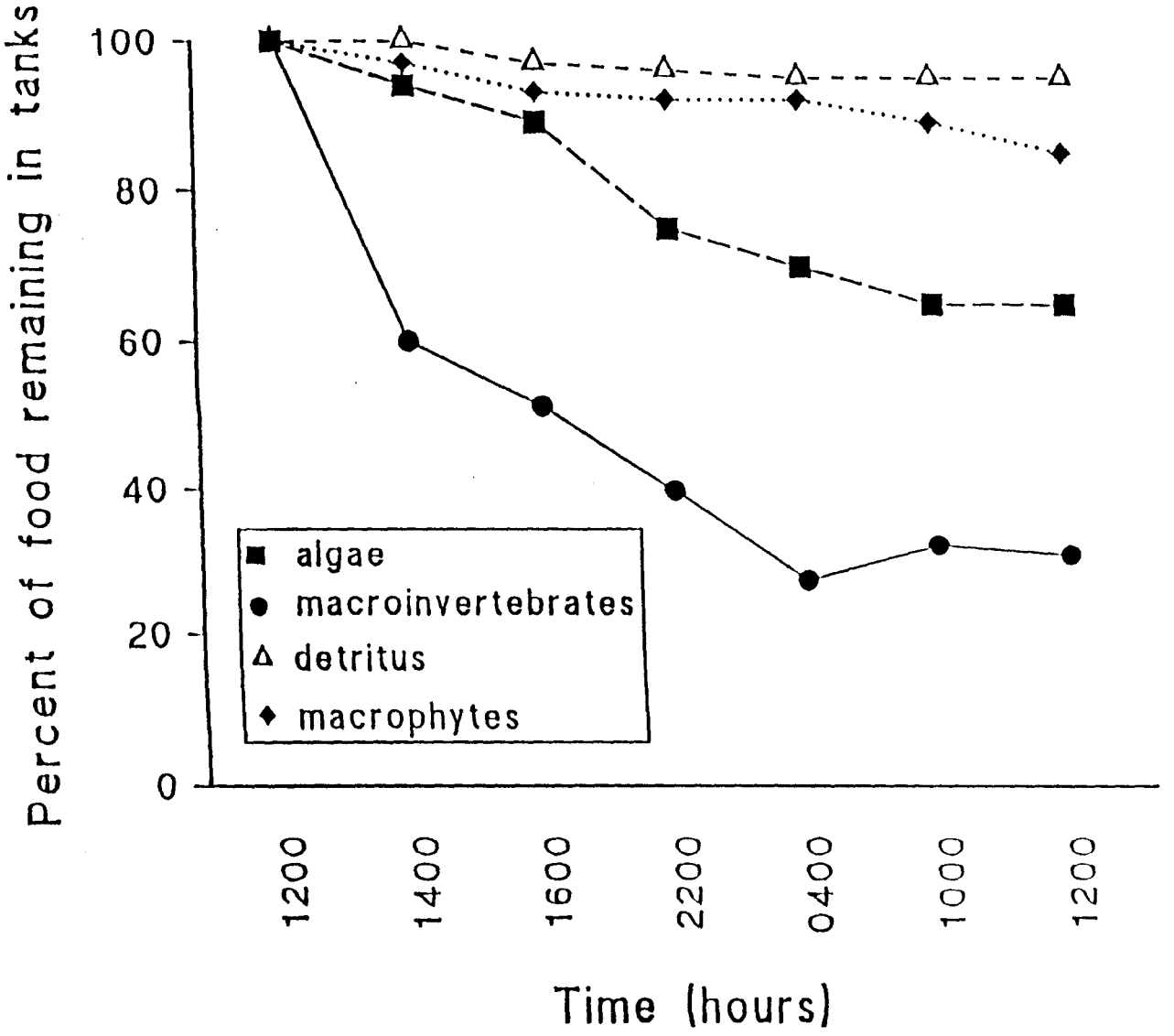

0.75
0.53
0.31
0.09
0.00
−0.13
−0.35
Preference Index
algae
macroinvertebrate
detritus
0.0
1.2
2.4
3.6
4.8
6.0
Crayfish Wet Weight (g)

Figure 9. Percent of food observed remaining in the five experimental tanks during the diurnal study. Intermediate data points are estimates.


Percent of food remaining in tanks
100
80
60
40
20
0
algae
macroinvertebrates
detritus
macrophytes
1200
1400
1600
2200
0400
1000
1200
Time (hours)

percent of food remaining in the experimental tanks at hours 1000 and 1200 was due to finding macroinvertebrates that were "hidden" from view (under clumps of algae, detritus, macrophytes, or the crayfish itself) during the 0400 observation, but were seen in subsequent observation periods (Figure 9).

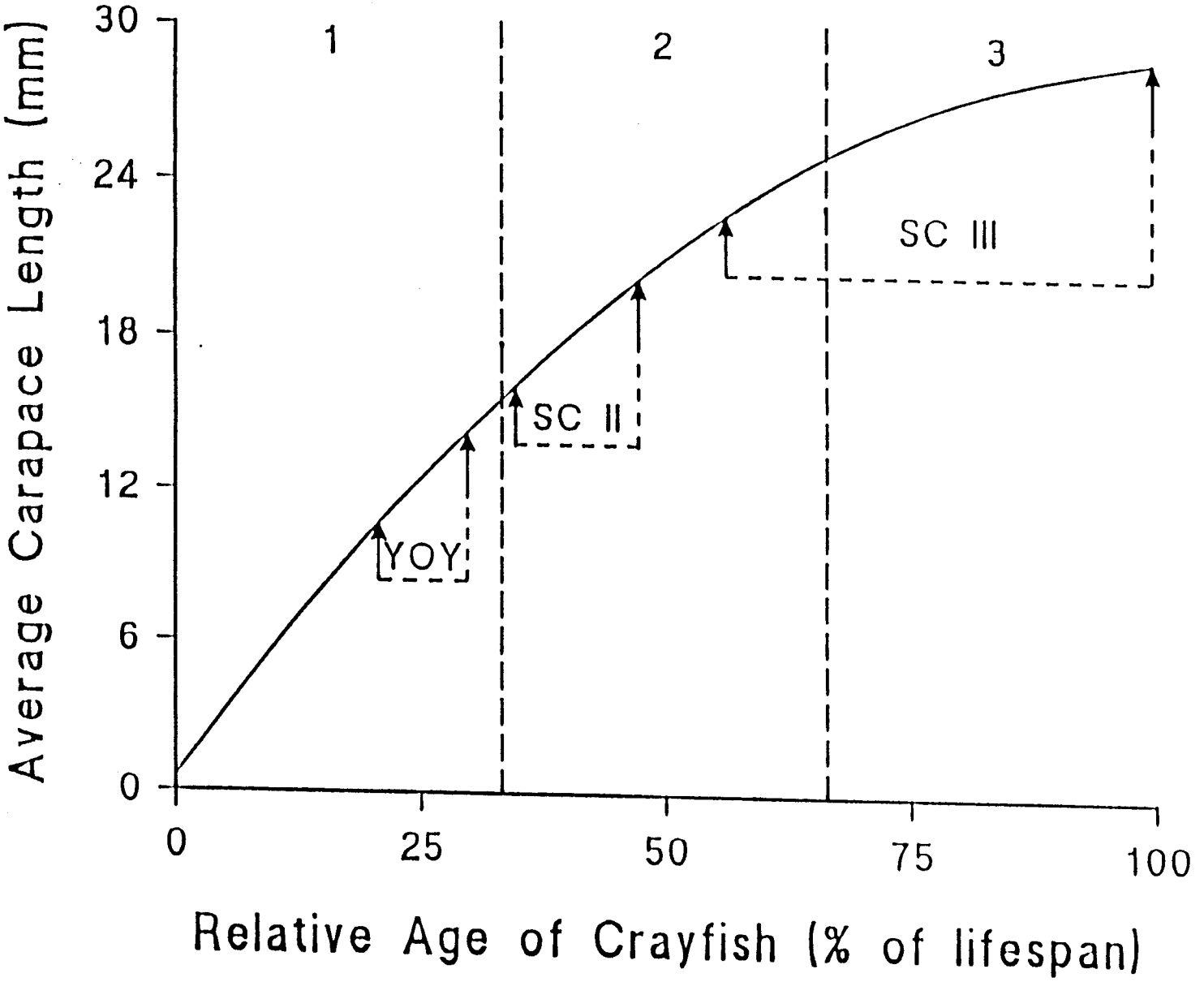
CHAPTER V

DISCUSSION

Growth of crayfish

Crayfish have indeterminate growth (based on growth increment and molt frequency) (Taylor 1990), so under ideal laboratory conditions, all size classes of crayfish would be expected to grow when they are not limited by food availability. However, in my 61-day growth rate study, size classes II and III exhibited little or no growth. Examination of an *O. propinquus* growth curve, using carapace length as an indication of growth during the lifespan of a crayfish (Figure 10), reveals the reason behind this result. It is evident from this figure that the rate of growth for size class I is greater than that for the adult crayfish. Based on this curve, it is expected that young-of-year crayfish will have a much higher growth rate (expected growth = 1.75 mm/61 day interval) than older crayfish who ultimately "maintain" their size as adults (size class II expected growth = 1.40 mm/61 days; size class III expected growth = 0.50 mm/61 days). In this study, crayfish in size classes I and III responded according to the growth curve as size class I sustained the highest growth rates (control mean carapace length increase = 2.5 mm), followed by size classes II and III (control mean

Figure 10. Growth curve of *O. propinquus* using average length of cephalothorax per relative age (percent of crayfish lifespan) of male and female crayfish (as reported by Van Deventer 1937; Creaser 1934; Vannote 1963; and YOY data from Quinn and Janssen 1989). Arrows indicate carapace size ranges for crayfish from this study. Numbers 1, 2 and 3 represent approximate years of crayfish life.


Average Carapace Length (mm)
30
24
18
12
6
0
1
2
3
SC III
SC II
YOY
0
25
50
75
100
Relative Age of Crayfish (% of lifespan)

carapace length increases = 0.07 mm and 0.02 mm, respectively). It was anticipated that because size class III were already the largest crayfish found in the lake, they would simply "maintain" their current size with little or no increase. Members of size class II, however, were expected to show some growth since they were not limited by food availability. The crayfish may have been stressed (especially during 61 days of growth measurements in the laboratory) in their artificial environments and responded differently than they might have in their natural habitats.

Individuals of size class I grew more rapidly when supplied with macroinvertebrates as a food source, likely because of the higher caloric and protein content of macroinvertebrates relative to algae or detritus treatments (Table 5). The fact that size classes II and III did not exhibit stimulated growth on high protein diets, suggests older individuals have different nutritional requirements than young-of-year crayfish. Benavides *et al.* (1994) found that the temperate herbivorous fish, *Aplodactylus punctatus* (Pisces, Aplodactylidae), increased its ability to assimilate algae as it grew, thus shifting from an omnivorous to a herbivorous diet. This may explain results of previous crayfish studies which showed that young-of-year crayfish fed more extensively on animal material than plant material or detritus (Vannote 1963; Momot *et al.* 1978). It is also possible that physiological changes play a role in the shift

TABLE 5

Caloric values for organisms

Ecological position	Taxa	Calories per gram ash-free dry weight
Periphyton		
	Cladophora sp.	4520 5170 ± 580[b]
Detritus (stream)		
	plant roots	4494.3 ± 99.2[a]
	composite leaves	4783.7 ± 250.0[a]
	Acer sp.	5290
	Quercus sp.	5257.0 ± 238.0[b]
Macroconsumers		
	Diptera spp.	6050 ± 129[b]
	Tenebrio molitor	6314 ± 516[c]
	Hydropsyche sp.	6375 ± 842.3[a]
	Neophylax sp.	5982 ± 390.1[a]
	Chironomidae	6050 ± 129[b]

Source: K.W. Cummins and J.C. Wuycheck, Caloric equivalents for investigations in ecological energetics. *Internationale Vereinigung Fur Theoretische Und Angewandte Limnologie. Komitee Fur Limnologische Methoden, Veroffentlichung* No. 15, 1971.

Notes: (a) plus or minus range, i.e. difference between high and low values
(b) standard deviation
(c) two standard deviations

in nutritional requirements exhibited by crayfish. Loyajavellana *et al.* (1994) compared the foregut of the tropical fresh-water crayfish, *Cherax quadricarinatus* Vonmartens, during development from embryonic larva to adult. They found that major ontogenetic changes occurred in the gastric mill dentition, therefore, natural food types appropriate for the various life history stages could be inferred from the morphology of the gastric mill dentition of those stages.

Overall, growth rate results of my study were similar to those reported by Hill *et al.* (1993) who conducted laboratory growth studies on three species of crayfish (*O. virilis, O. propinquus* and *O. rusticus*) from Trout Lake, Winsconsin. Their crayfish were offered one of five diets: invertebrates, macrophytes, detritus, periphyton or a combination. Hill *et al.* (1993) found that for all three species of crayfish, diets of invertebrates or the combination produced the highest growth rates. They also found that the three crayfish species exhibited little or no growth over 55 days when fed macrophytes, detritus or periphyton.

Crayfish dietary preference. All crayfish from this study showed a significant preference for macroinvertebrates when given equal access to algae, detritus, and macroinvertebrates. These results were supported by observations of the 24-hour study where crayfish chose macroinvertebrate prey as a primary preference over the algae or detritus throughout a

24 hour observation period. This is consistent with several studies which found adult crayfish to selectively consume snails even when algae or macrophytes were available (Hanson *et al.* 1990; Lodge and Lorman 1987; Covich 1977).

Alternately, Capelli (1980) reported *O. propinquus* to be an opportunistic scavenger that selected in favor of some items when they were seasonally available. Gut contents of crayfish in Lake Michigan contained relatively few macroinvertebrates (18% biovolume) reflecting the apparent low availablity of this "preferred" food item to the crayfish in this habitat.

While it was evident that crayfish from the Lake Michigan habitat consumed algae in greater quantities (58% biovolume) than either detritus or macroinvertebrates, they may not be simply opportunistic feeders. It is, perhaps, necessary for crayfish to consume more algae to compensate for its lower nutritional quality in relation to other energy sources. Studies with the crayfish *Pacifastacus lenuisculus* (Moshiri and Goldman 1969), in which animals were fed chicken and aquatic vascular plants, showed that although the plant-fed individuals had lower assimilation efficiencies than those on animal diets, they compensated by ingesting more plant material per unit time.

The preference of macroinvertebrates for all size classes may be related to the higher quality of nutrition provided by macroinvertebrate prey (higher caloric value, higher

protein/fat content) (Table 3). It may also be an innate response, ensuring that juvenile crayfish ingest enough protein to molt frequently enough to rapidly surpass the size threshold beyond which they are no longer susceptible to predation by yellow perch, other fish or adult crayfish. Though still exhibiting a taste preference for macroinvertebrate prey when this food source is readily accessible, perhaps a reproductively mature crayfish changes its feeding strategies when macroinvertebrates are scarce. It has been shown that large, mobile invertebrates were capable of avoiding predation by crayfish (Abrahamsson 1966; Tcherkashina 1977), potentially making predation an energetically costly pursuit. If protein requirements are lower for adults than for juveniles, perhaps adults conserve energy (in habitats rich in algae, macrophytes and detritus) by grazing and browsing rather than competing for, pursuing and capturing macroinvertebrate prey.

Impacts of the Zebra Mussel Invasion

Prior to the invasion of the zebra mussels in Lake Michigan, the lake food web was plankton-driven and benthic primary and secondary production was low (Zenchak 1993); crayfish in the rock areas were potentially limited by macroinvertebrate food. Since 1991, zebra mussels have effectively cleared the water column of phytoplankton, and increased light penetration to the bottom of the littoral zone stimulating both primary and secondary production (Bradford

and Tuchman 1994). It is, therefore, expected that crayfish densities will increase due to the increase in available macroinvertebrates, algae, and detrital food resources (e.g. zebra mussel feces and pseudofeces). There is evidence that total crayfish densities in the rock reefs have increased, even though zebra mussels have decreased rock interstitial spaces used for crayfish shelter (Bradford and Tuchman 1994).

CHAPTER VI

SUMMARY AND CONCLUSIONS

All crayfish showed a preference for macroinvertebrates when given equal access to the three dietary treatments. However, the growth rate study, supported by results of gut content analyses, suggests that benthic algae are the key component sustaining crayfish in the Lake Michigan rocky areas, and that crayfish in these habitats feed on what is most available. In terms of growth rates, young-of-year crayfish were the only group to show a significant effect of food treatment on growth, stimulated by diets of animal protein. The larger crayfish (> 1 yr) exhibited no significant effect of food treatment on mean percent weight change and essentially maintained their weights throughout the study. Secondary production in young-of-year crayfish in the Lake Michigan rock areas, therefore, may be limited by low availability of invertebrate prey.

In the littoral zone food web, crayfish are an energetically important link between algae and the top carnivore, yellow perch. However, the rocky areas have undergone an abrupt change since the recent invasion of the zebra mussel (*Dreissena polymorpha*). Since 1992, densities of these exotic molluscs have increased and light intensities on

the rock regions have drastically increased (Bradford and Tuchman 1994).

The increased light penetration, presumably due to the filtering of phytoplankton from the water column by zebra mussels, stimulated benthic algal production on the rock sites (Bradford and Tuchman 1994). Along with the algae, increases in the macroinvertebrate and detrital densities are expected to have a positive effect on crayfish densities in the rock regions. This increase in densities of benthic algae and macroinvertebrates could stimulate young-of-year crayfish secondary production increasing their densities and producing larger individuals more capable of escaping predation and/or cannibalism by other crayfish. The additional benthic filamentous algae will serve as both shelter and food source enabling crayfish populations to flourish.

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The thesis is, therefore, accepted in partial fulfillment of the requirements for the degree of Master of Science.

15 Nov 94
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